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A comparison of annual transpiration and productivity in monoculture and mixed-species Douglas-fir and red alder stands

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ABSTRACT

Although much is known about drivers of productivity in Douglas-fir and red alder stands, less is known about how productivity may relate to stand transpiration and water use efficiency. We took advantage of a 15-year-old experiment involving Douglas-fir (*Pseudotsuga menziesii*) and red alder (*Alnus rubra*) in the western Cascade Range of western Oregon to test the following hypotheses: (a) more productive stands transpire more water, (b) the relationship between productivity and transpiration differs between species, and (c) the relationship between productivity and transpiration differs between sites varying in soil moisture and fertility. Furthermore, the experimental design included alder, a facultative nitrogen-fixing species, which could also affect fertility. Fixed area plots (20 × 20 m) were planted as monocultures of each species or in mixtures at a common density (1100 trees ha^{-1}) in a randomized-block design. Transpiration of Douglas-fir and red alder was measured using heat dissipation sensors installed in eight trees per plot and scaled to the plot level based on sapwood basal area for each species. Although up to 53% of the variability in tree transpiration was explained by basal area, irrespective of species or site conditions, the two stands with the highest biomass and sapwood basal area did not transpire the most. Instead of more productive stands transpiring more water, the greatest variability in both productivity and transpiration was determined by site conditions and to a lesser degree, species composition. For example, 70% of the variation in tree biomass increment (TBI) was determined by leaf area index, which was much higher at the site with higher fertility and soil moisture ($p < 0.05$). Despite marked phenological and physiological differences, Douglas-fir and red alder performed similarly. Only 19% of annual water use of Douglas-fir occurred between October and March when alder was leafless. Also, there was no evidence of a fertilization effect of the nitrogen-fixing red alder on the Douglas-fir: the nitrogen concentration and N-isotopic ratio of Douglas-fir needles did not differ whether trees were grown in monoculture or in mixtures with red alder. We conclude that lower soil fertility and contrasting microclimate at one site relative to the other suppressed NPP while maintaining higher transpiration, thus reducing water use efficiency.

1. Introduction

Potential tradeoffs between productivity and resource use efficiency are critical to understand, especially considering that forest management in the 21st century may need to account for multiple ecosystem services, such as maintaining adequate water supplies (Likens and Franklin, 2009). In this regard, a two-species interaction that increases ecosystem productivity might not result in a parallel increase in ecosystem water use (Vanclay, 2009). In fact, water use efficiency (WUE) might be higher in a mixed-species stand due to differential use of water resources in time and space, also known as complementary resource use (Kelty, 2006). Land managers may need to decide among strategies that differentially affect productivity, biodiversity, and water resources. There is little available literature, however, on how these factors interact with one another despite the long-standing debate about hydrological impacts of forest management practices (Andreassian, 2004).

Forest plantations are typically grown as monocultures in part because trees in mixed-species stands grow irregularly in response to intraspecific and interspecific competitive relations (Freckleton and Watkinson, 2001). For example, in the Pacific Northwest,

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Abbreviations: WUE, water use efficiency; LAI, leaf area index; TBI, tree biomass increment; NPP, net primary productivity.

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young red alder (*Alnus rubra* Bong.) is considered by many to be a weed within early seral Douglas-fir stands (*Pseudotsuga menziesii* (Mirb.) Franco) because it grows faster and so competes with Douglas-fir seedlings for light (Shainsky and Radosevich, 1992). Thus, forest managers generally prescribe treatments that encourage Douglas-fir monocultures. From an ecological standpoint, however, emphasis on forest conservation and ecosystem services in plantation forestry (Carnus et al., 2006) has placed an increasing value on mixed-species managed stands (Ehrlich and Wilson, 1991; Naeem et al., 1994).

Researchers have predicted that tree species mixtures in plantation forestry can exhibit higher stand-level productivity than monocultures if they can extract more light, water, or nutrients (Menalled et al., 1998). In a subtropical rain forest, two fast-growing tree species planted in mixtures used more nutrients because timing of peak uptake differed by several months (Richards and Schmidt, 2010). In northern temperate forests, high productivity in high-density mixtures of fast-growing Douglas-fir and slower-growing western hemlock was attributed to better use of site resources (Amoroso and Turnblom, 2006). Similarly, when nitrogen-fixation facilitates growth of neighbor plants we might expect higher stand-level productivity (Kelty, 2006). However, nitrogen-fixation will only be beneficial to total ecosystem productivity if it enhances access to limiting resources. Existing observations of Douglas-fir and red-alder interactions (Berntsen, 1961; Rothe and Binkley, 2001; Rothe et al., 2003) highlight this effect: in nitrogen-poor sites red alder improves productivity of Douglas-fir, but in sites where nitrogen is not limited, red-alder reduces Douglas-fir productivity (Binkley, 2003). This latter observation suggests that direct competition for another resource is affecting overall productivity.

There is comparatively little information available concerning water competition, but there are reasons to expect that Douglas-fir and red alder have different niches in regards to water use. Both species are high water users when young (Moore et al., 2004), but Douglas-fir is more tolerant of dry soils (Chan et al., 2003) and this, plus its evergreen habit, means it has the potential to transpire through a much greater portion of the year than red alder. In contrast, red alder has a higher leaf-specific hydraulic conductance (Bond and Kavanagh, 1999) and has deeper roots than Douglas-fir at the sapling stage (Hibbs et al., 1994). Red alder is also more productive than Douglas-fir during early stages of stand development, often out-competing Douglas-fir for light (Chan et al., 2003).

Although much is known about drivers of productivity in Douglas-fir and red alder stands, less is known about how productivity may relate to stand transpiration and WUE. We tested the following hypotheses: (a) more productive stands transpire more water, (b) the relationship between productivity and transpiration differs between species, and (c) the relationship between productivity and transpiration differs between sites with contrasting available resources. To determine whether more productive stands transpire more water, we examined differences in tree transpiration as a function of basal area. We also examined differences in annual transpiration between stands that differed in net primary productivity (NPP), leaf area, and sapwood area. Because of expected seasonal and physiological differences in transpiration between Douglas-fir and red alder, we compared monoculture and mixed-species stands to see whether the relationship between productivity and transpiration was indeed species-specific. Because WUE can also change with resource availability, we compared two sites differing in solar radiation, soil moisture, and fertility.

2. Material and methods

2.1. Study area

This study took place at the H.J. Andrews Forest in the western Cascade Range of Oregon. The climate is characterized as maritime with wet winters and dry summers (mean annual rainfall = 2300 mm). Mean monthly temperature ranges from about 1 °C in January to 18 °C in July. Soils are classified predominantly as gravelly clay loam.

2.2. Replacement series

We compared annual tree productivity in the most recent four years and in the 15 years since planting (e.g., biomass, leaf area, basal area) to annual total stand transpiration in study plots that were part of a 'replacement series' experiment (Radosevich, 1987) initiated in 1986 (Radosevich et al., 1997). A randomized-block design was employed with an assortment of treatments at a fixed density with varying proportions of Douglas-fir and red alder (D'Amato, 2002; Grotta, 2002). Trees were planted in 3 × 3 m spacing (1100 trees ha^{-1}) in 20 m × 20 m plots. Hence, there was a 5 × 5 tree (25 trees/plot) interior grid surrounded by

Table 1

Stand-level attributes by plot location and treatment, including the number of live trees remaining from the 25 initially planted, stand total basal area (BA), biomass, sapwood basal area (SBA), leaf area index (LAI), and leaf area to sapwood area ratio (LA:SA). The relative proportion of red alder (RA) biomass and SBA is shown for mixed-species plots. Average Douglas-fir (DF) sapwood depth is also provided along with plot average tree diameters (DBH) for RA and DF, respectively. Annual tree biomass increment for the year 2002 (TBI) is a measure of tree productivity. Total annual transpiration (T) is derived from sap flow measurements. Water use efficiency (WUE) is computed as TBI/T in g C per g H_2O.

Stand attribute	Units	U-site				L-site			
		Mixed	Mixed-delay	Douglas-fir	Red alder	Mixed	Mixed-delay	Douglas-fir	Red alder
# Live trees	Count	19	18	23	22	24	20	23	20
Total BA	m^2 plot^{-1}	0.22	0.19	0.25	0.24	0.29	0.22	0.27	0.40
Total biomass	kg	1126	1019	1354	1692	2002	1213	1413	2396
Relative RA biomass	%	35	5			91	18		
Total SBA	m^2 plot^{-1}	0.21	0.17	0.22	0.26	0.26	0.19	0.23	0.28
Relative RA SBA	%	36	10			87	21		
LAI	m^2 m^{-2}	1.75	0.88	2.39	2.46	4.74	3.02	5.51	3.65
LA:SA ratio	m^2 cm^{-2}	0.34	0.21	0.44	0.39	0.72	0.64	0.95	0.52
*DF sapwood depth	cm tree^{-1}	4.15	4.52	3.63		1.77	4.22	3.81	
RA DBH	cm tree^{-1}	11.16	5.80		12.45	16.68	8.29		15.80
DF DBH	csm tree^{-1}	15.10	14.37	12.70		7.23	14.43	12.89	
TBI	g m^{-2} yr^{-1}	384	461	557	538	717	637	673	717
Annual T	mm yr^{-1}	96	85	108	130	107	88	95	104
WUE	g g^{-1}	0.0040	0.0054	0.0051	0.0041	0.0067	0.0072	0.0071	0.0069

* It was determined that RA did not contain heartwood.

two additional rows of trees as a buffer. Briefly, there were two types of mixed-species plots planted in 50:50 proportions, "mixed" and "mixed-delayed." In the "mixed" plots, both species were planted in 1986; in the "mixed-delayed" plots, red alder was planted five years later. There were two replicate sites, separated by 2.3 km, with elevations of 660 and 760 m, at the "L-site" and "U-site," respectively. The U-site faced west, while the L-site faced north. Each site included four plots, one each of the following types: Douglas-fir monoculture, red alder monoculture, mixed, and mixed-delayed. (Therefore this study involved a total of eight plots, two of each type). Current proportions of the two species in mixed and mixed-delayed plots were no longer 50:50 at the time of this study because some mortality had occurred (Radosevich et al., 2006).

2.3. Stand characteristics

Diameters of all trees in the plot interiors were measured in July 1998 and 2002 at breast height (1.37 m) and also at the height of sap flow sensors (2002 only). Sapwood depth in all Douglas-fir trees in the plot interiors was measured with visual assessment of a 5-mm increment core taken at ~1.2 m or below the lowest branch. The difference in color is clearly discernable; sapwood appears darker and wetter than heartwood. Because sapwood in red alder cannot be distinguished from heartwood visually, we used a safrinin dye injection method to aid in the determination of sapwood depth (Kutscha and Sachs, 1962; Booker, 1984; Bamber and Fukazawa, 1985). After injecting dye in seven trees (dominant and subdominant, two replicates each), we found no evidence of heartwood, and thus concluded that the wood of these young alders consisted entirely of sapwood.

Leaf area (leaf area index [LAI]) was estimated at four random locations dispersed within each plot using a LAI 2000 (Licor Inc., Lincoln, NE, USA) equipped with a 90° mask on the optic sensor, leaving an open quartile facing the plot centers. The lowest zenith angle was removed to avoid including topography, stems, and other obstructions as leaf area. Measurements were repeated monthly for 6 months in 2001: on April 5, May 4, June 20, July 23, August 29, and September 10. Prior to alder leaf emergence in early spring of 2002 (March 22), LAI measurements were made to compare LAI with and without alder leaves. Diffuse light conditions are considered ideal for light transmittance based estimates of LAI (Kucharik et al., 1998), and so the March, April, and May measurements were taken during the day under uniform overcast sky conditions and the June, July, August, and September measurements were taken in the evening at dusk under uniform clear sky conditions. We detected no discernable phenological pattern in LAI, so the six replicate measurements in 2001 (excluding March 2002) were averaged. Additional stand characteristics are described in Grotta (2002) and D'Amato (2002).

Foliar biomass, total aboveground wood and bark biomass, and belowground coarse root biomass for the years 1998 and 2002 was estimated based on the diameter at breast height (Douglas-fir), and both diameter at breast height and tree height (red alder) using species-specific equations (Gholz et al., 1979). As a proxy for total annual net primary productivity of trees excluding fine root turnover, tree biomass increment (TBI) was determined as the annual change in total biomass of stems, bark, coarse roots, and leaves, assuming uniform growth throughout the 4-year period.

2.4. Sap flow

Eight trees per plot were selected randomly for sap flow measurement, four of each species in mixed plots, for a total of 64 trees for the entire experiment. Trees having more than two dead neighbors were not selected, except one tree in a red alder monoculture plot had four dead neighbors. We used the thermal dissipation sap

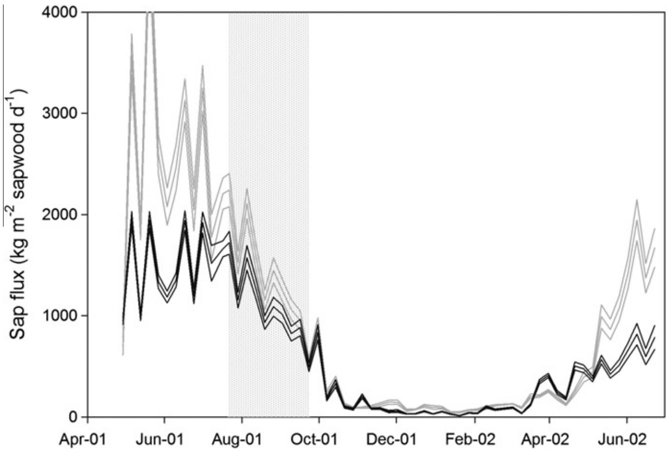

Fig. 1. Mean weekly total sap flux density of Douglas-fir (black, $n = 32$ trees) and red alder (gray, $n = 32$ trees) in kg water per m^{-2} sapwood area per day through an annual cycle. Means are for all plots combined because there were no differences in trends between mixed and monoculture plots. Standard error lines are shown above and below mean values. The shaded area highlights the period of greatest soil moisture deficit.

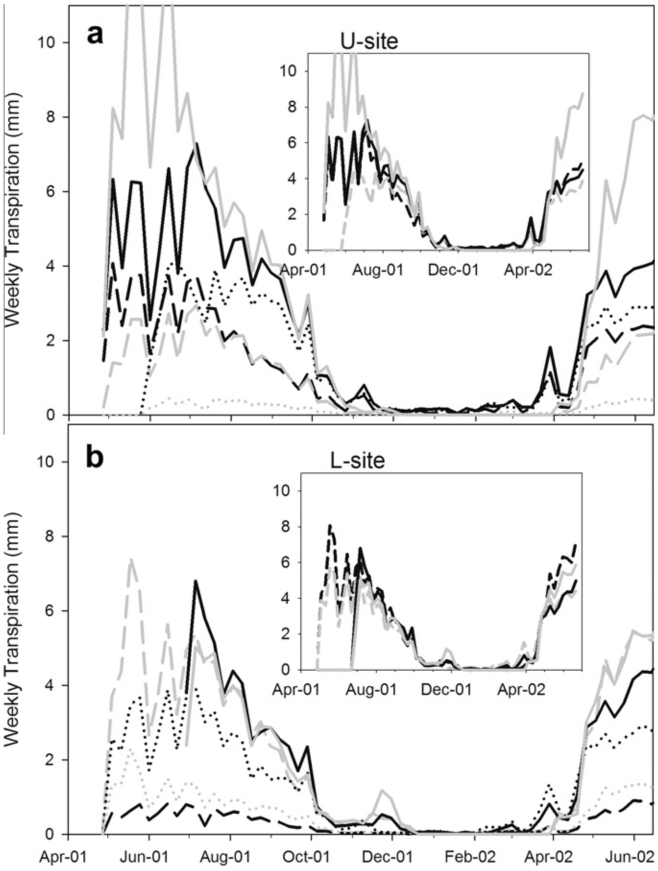

Fig. 2. Weekly totals of transpiration in mm by plot and species at the (a) U-site and (b) L-site in Douglas-fir monocultures (solid black) and red alder monocultures (solid gray). Transpiration in mixed plots is split between the two species with Douglas-fir (dashed black) and red alder (dashed gray) indicating each species in the mixed-species plots. Likewise transpiration in mixed-delayed plots is split between Douglas-fir (dotted black) and red alder (dotted gray). Inset figures summarize transpiration by plot type (mixed = dashed black line, mixed-delayed = dashed gray line, Douglas-fir = solid black line, red alder = solid gray line).

flow technique (Granier, 1987). Sensors were constructed in our laboratory as described by Phillips et al. (1997). Sap flow sensors (one per tree) were installed at a height of 0.5–1.0 m, below the height of the lowest live branches. Instantaneous measurements taken at 30-s intervals were averaged every 20 min and recorded on a data logger (CR10X, Campbell Scientific, Logan, UT, USA).

Measurements were scaled from individual sensors to whole-tree average flux per unit sapwood per day using the methods described in Moore et al. (2004). Briefly, the total flux per tree was divided by the total sapwood area to estimate average flux per unit sapwood area for each tree. We also expressed transpiration per tree as the flux per unit sapwood of that tree ($n = 1$ sensor) multiplied by the total tree sapwood area. These calculations were performed for each 20-min time step. Total daily fluxes are the summation of the 20-min observations. Trees were instrumented April–June 20, 2001. Measurements continued until July 1, 2002. A correction was made for sap flow after April 27, 2002, because of temporal sampling errors (Moore et al., 2010).

2.5. Environmental measurements

Soil moisture was monitored as volumetric water content periodically (two- to four-week intervals) in June through August of each year at 32 locations (four locations per plot, randomly located within the plot interiors) using time domain reflectometry (Model 1502C, Tektronix, Inc., Beaverton, OR, Gray and Spies, 1995); 45- and 90-cm rods were installed vertically at each location. In addition, predawn leaf water potential (Ψ_p) was measured bimonthly (on 6/13, 6/28, 7/12, 7/26, 8/7, 8/31, 9/6, and 9/21 of 2001) using a pressure chamber (PMS Instruments, Corvallis, OR), with four replicate twig samples per plot (two from each species in mixed plots).

Sunlit leaves were clipped from the tops of trees (four trees of each species per plot, with three replicate leaves each, pooled to create a single sample per tree) in September 2001. They were subsequently oven dried, ground to a fine powder, and analyzed for bulk nitrogen concentration and nitrogen isotopic ratio of $^{15}N/^{14}N$. Soil cores (5-cm diameter) were collected at a depth of 10–15 cm at four locations per plot in late July 2002. They were subsequently oven dried, sieved through a 2-mm mesh, and ground to a fine powder. Both leaf and soil N concentration and $^{15}N/^{14}N$ ratios were analyzed using an elemental analyzer (ESC 4010, Costech Analytical Technologies, Valencia, CA, USA) in line with an isotope ratio mass spectrometer (Delta Plus, Finnigan, Bremen, Germany) at the Integrated Stable Isotope Research Facility (ISIRF) at the Environmental Protection Agency in Corvallis, OR. The N isotopic ratios were standardized to atmospheric air and expressed as $\delta^{15}N$. Precision for $\delta^{15}N$ was assessed using a National Institute of Standards and Technology certified standard, with an average standard deviation of 0.08.

2.6. Analysis

All statistical analyses were conducted using S+ software (TIBCO Software Inc., Palo Alto, CA). Differences among means were tested at an alpha level of 95% ($p < 0.05$). Stepwise multiple regression was used to determine the relationship between tree transpiration and basal area, and whether it differed by species, site, or treatment ($n = 64$ trees); and to test stand-level relationships between TBI and transpiration, and whether they differed by site. Because stand density can affect site-level productivity and transpiration, multiple regression was also used to determine how stand-level annual transpiration related to total biomass, sapwood area, leaf area, and leaf area to sapwood area ratio ($n = 8$ stands).

Seasonal variation in sap flux rates over a 12-month period were plotted on a weekly basis for Douglas-fir and red alder ($n = 32$ trees per species). Periods when standard errors were not overlapping highlighted species-specific differences. Of particular interest was the period between October and March when red alder was dormant. Given seasonal and physiological differences between Douglas-fir and red alder, we compared transpiration, TBI, and the ratio between them (i.e., WUE) in monoculture stands of Douglas-fir ($n = 2$) and red alder ($n = 2$) and mixed-stands of both species ($n = 4$). Multiple regression was used to compare WUE between sites and stands on the basis of percent biomass of red alder, because species proportions can have an effect on site-level transpiration and tree productivity.

Edaphic conditions were expected to vary between sites, particularly during the late summer when soil moisture was the least, because the U-site was on a west-facing slope and the L-site was on a north-facing slope, which affects incoming solar radiation. We compared soil moisture and predawn leaf water potential between plots and sites using nested ANOVA. To test for differences in site fertility, we compared soil and leaf nitrogen concentration. Finally, to determine whether a possible signal of nitrogen-fixing red alder is seen in Douglas-fir in mixed-species stands though changes in soil nitrogen isotopic ratios, we compared d15N of Douglas-fir needles between monoculture and mixed-species plots using ANOVA.

3. Results

Approximately 15 years of differential mortality and growth had changed the proportion of Douglas-fir and red alder from the 50:50 mixture in the initial planting (Table 1). Of the 25 trees planted per plot, between one and seven trees died. In general, more alder died than Douglas-fir. Either on a sapwood area or biomass basis, three of the four mixed plots had shifted towards Douglas-fir dominance (Table 1); whereas, one mixed plot was dominated by red alder. The LAI was 2.3 times higher at the L-site and tended to be lower in plots with higher mortality (Table 1). Mean diameters of trees ranged between 5.8 and 16.7 cm in three of the four mixed plots where Douglas-fir trees were bigger than red alder. Douglas-fir monocultures also had the highest LA:SA and total biomass, but this did not result in the highest annual transpiration.

Despite the wide-ranging plot characteristics, annual transpiration did not vary greatly between plots. Overall, red alder

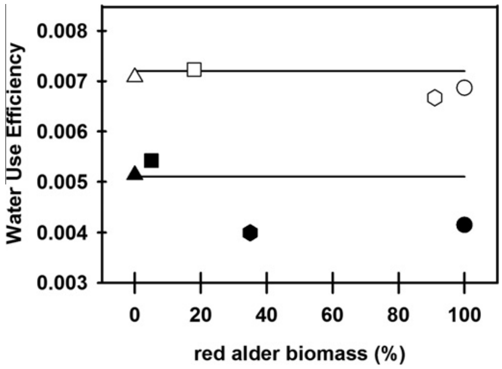

Fig. 3. Water use efficiency as the ratio of tree biomass increment and transpiration (TBI/T) in g C per g H_20 at the U-site (closed symbols) and L-site (open symbols). Species proportions on the x-axis are expressed by proportion of red alder biomass (%) in each plot; i.e., plots with 0% alder biomass are Douglas-fir monocultures; plots with 100% alder biomass are red alder monocultures (see Table 1). Lines represent mean values for each site estimated using multiple regression. Slopes were not significantly different from zero.

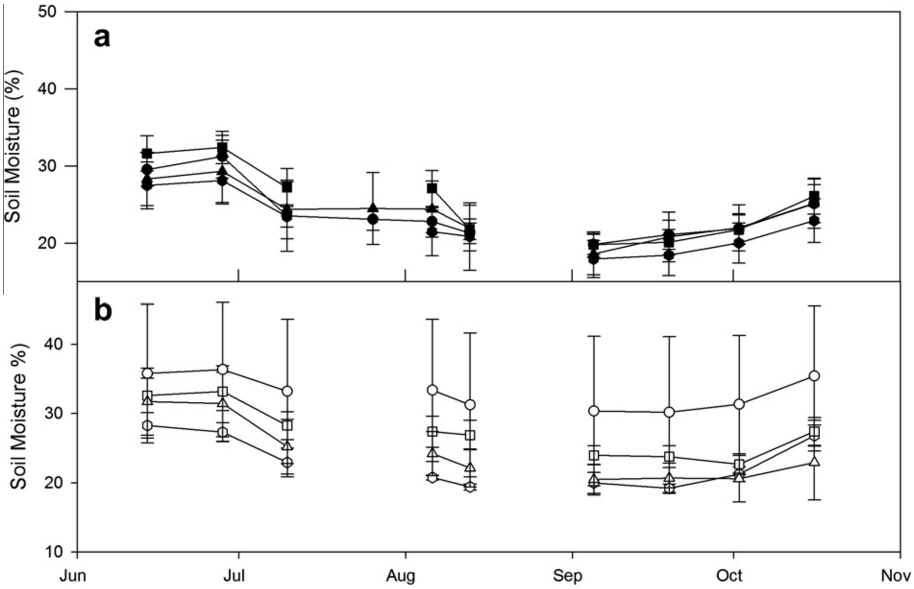

Fig. 4. Mean volumetric soil moisture (%) in the top 45 cm of soil for each plot (standard error bars for $n = 4$ replicates per plot) during the period between June 14 and October 16, 2001 at the (a) U-site and (b) L-site. Symbols indicate plot type including Douglas-fir (triangle), red alder (circle), mixed-species (hexagon), and mixed-delayed (square).

transpired more on an annual basis than Douglas-fir. At the U-site, the Douglas-fir monoculture plot transpired 108 mm annually, compared with 130 mm in the red alder monoculture. At the L-site, the Douglas-fir monoculture transpired 95 mm annually, compared with 104 mm in the red alder monoculture. The minor differences between Douglas-fir and red alder monocultures of about 22 and 9 mm (equates to 17% and 9% of annual totals) was no greater than the difference between sites of about 13 and 26 mm for Douglas-fir and red alder monocultures, respectively.

Despite seasonal differences in phenology, annual trends in sap flux were similar between the two species (Fig. 1). Temporal patterns in sap flux were also similar among all plots at both sites, differing only in magnitude according to the relative site dominance (Fig. 2). Peak sap flow was higher and occurred earlier in red alder (week of May 20) than in Douglas-fir (week of July 1). In late summer there was a sharp decline in sap flux rates of both species, presumably due to declining soil moisture and decreasing vapor pressure deficits (shaded area of Fig. 1). Although Douglas-fir is evergreen, its sap flux was nearly zero in the winter in response to very low vapor pressure deficits (Figs. 1 and 2). During the six months of October through March, the magnitude and pattern of sap flux was surprisingly similar between species, averaging 95 and 101 kg m^{-2} sapwood d^{-1} in Douglas-fir and red alder, respectively, which amounted to only 19% and 17% of annual fluxes occurring that half of the year. Notably, Douglas-fir showed an earlier spring rise in sap flux while red alder remained dormant (Figs. 1 and 2).

Large differences in WUE between the U-site and L-site were observed ($p < 0.01$, Fig. 3) and may relate to edaphic conditions such as microclimate or fertility. The L-site, located on a north-facing slope, had 50% greater WUE than the U-site located on a west-facing slope. At each site, there was no significant difference in WUE between plots, regardless of species composition. Soil moisture declined to a minimum value on September 5, 2001 (Fig. 4) and ranged between 13% and 25% at the U-site and 17% and 62% at the L-site in the top 45 cm of soil (Fig. 4a). In the top 90 cm, values of 14–45% and 12–61% at the U- and L-sites, respectively (Fig. 4b), indicated the soil was slightly wetter. There were no significant differences between plots or sites (ANOVA, $p > 0.05$) on the driest day of record, September 5, in predawn water potential (Fig. 5a) and soil moisture in the top 45 cm (Fig. 5b) and top 90 cm (Fig. 5c). The red alder plot at the L-site

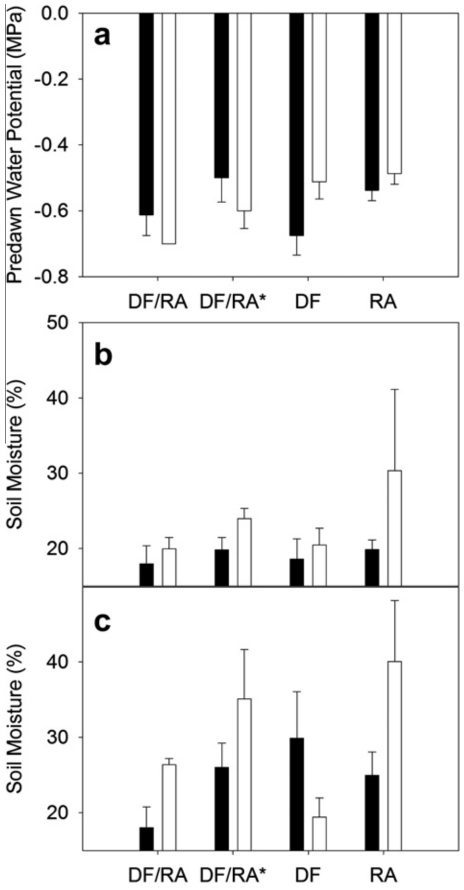

Fig. 5. Mean (a) predawn water potential (MPa) and volumetric soil moisture (%) in (b) the top 0–45 cm and (c) the top 0–90 cm by plot (standard error bars for $n = 4$ replicates per plot) at the U-site (black bars) and L-site (open bars) on September 5, 2001 when soil water deficits were the greatest (see Fig. 4). Douglas-fir = DF, red alder = RA, Mixed = DF/RA, mixed-delayed = DF/RA*.

had a small stream that ran through it, giving it high but variable moisture.

Overall, the L-site was 41% more productive (1998–2002), had more than double the leaf area index, and more than double the LA:SA ratio compared with the U-site (paired *t*-tests, $p < 0.05$). Each site had close associations between transpiration and total biomass (Fig. 6a), transpiration and sapwood basal area (Fig. 6b), and transpiration and leaf area index (Fig. 6c) that were independent from the other site ($p < 0.05$). In every case, the U-site was more tightly correlated than the L-site. For example, transpiration was related to LA:SA at the U-site ($r^2 = 0.52$), but not at all related to LA:SA at the L-site (Fig. 6d, $p > 0.05$). By contrast, TBI was more closely associated with transpiration (Fig. 6e) and sapwood basal area (Fig. 6f) at the L-site ($r^2 = 0.98$ and 0.97, respectively) than at the U-site ($r^2 = 0.41$ and 0.58, respectively). Across all sites and plots, leaf area index (Fig. 6g, $r^2 = 0.70$) and LA:SA (Fig. 6h, $r^2 = 0.58$) were the best overall predictors of TBI.

Site-level differences were likely related to fertility. The L-site had significantly greater soil N concentration than the U-site ($p = 0.02$, Fig. 7a), and the alder leaves had a higher N concentration than the Douglas-fir needles. Taking into account the total leaf area, N mass was also higher in the L-site. There was no difference in leaf N concentration between mixed and monoculture plots in either species. The L-site soils had a lighter $\delta^{15}N$ signature than the U-site ($p = 0.003$, Fig. 7b). Red alder was likely fixing nitrogen because the leaf $\delta^{15}N$ was significantly higher in the alder leaves than in Douglas-fir needles ($p < 0.0001$), yet there was no difference in Douglas-fir needle $\delta^{15}N$ between mixed and monoculture plots ($p = 0.67$). In all plots, soil nitrogen was isotopically heavier than the leaves.

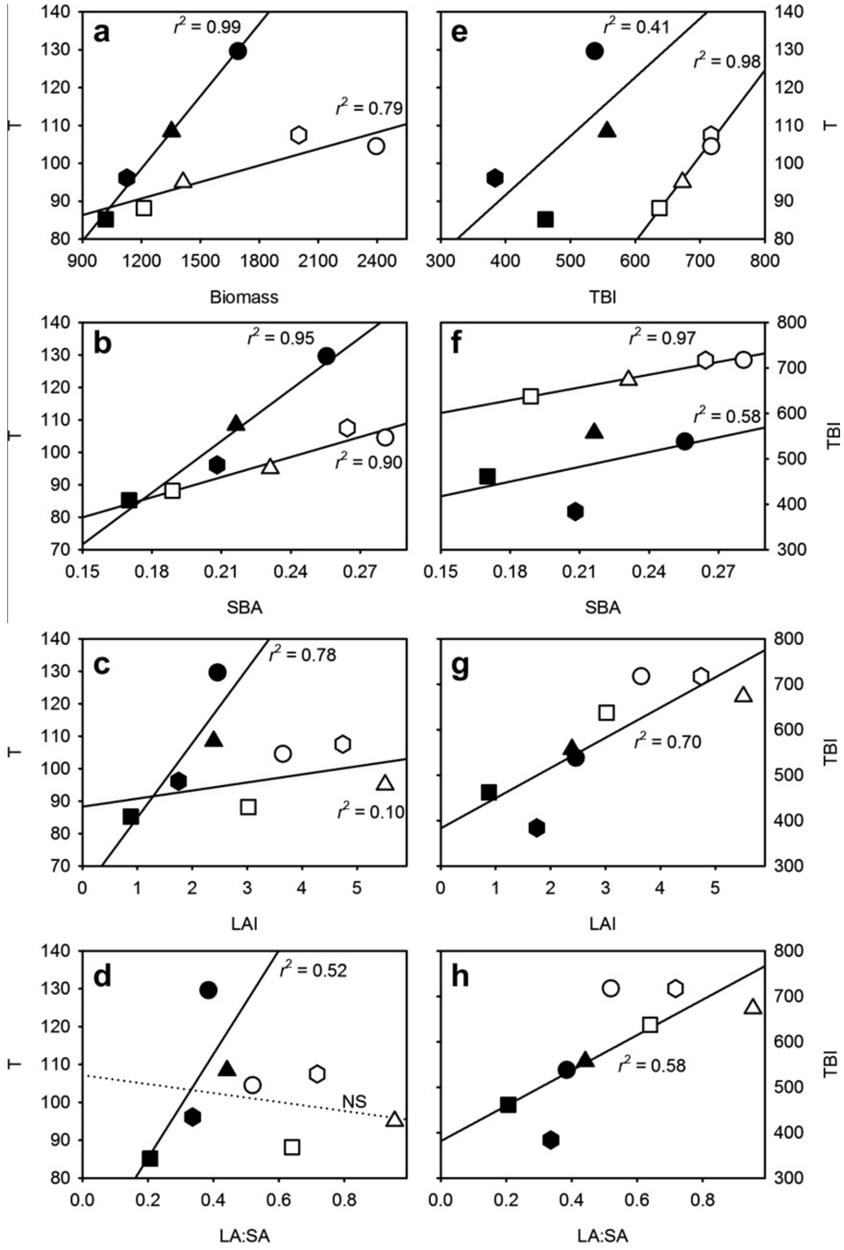

Fig. 6. The relationship between annual total transpiration (T, mm) and (a) biomass production (kg), (b) sapwood basal area (SBA, m^2), (c) leaf area index (LAI, $m^2\ m^{-2}$), (d) leaf area to sapwood area ratio (LA:SA, $m^2\ cm^{-2}$), and (e) tree biomass increment (TBI, $g\ m^{-2}\ yr^{-1}$) by plot at the U-site (closed symbols) and L-site (open symbols). Also shown is the relationship between TBI and (f) SBA, (g) LAI, and (h) LA:SA. Symbols indicate plot type including Douglas-fir (triangle), red alder (circle), mixed-species (hexagon), and mixed-delayed (square). Lines represent least squares regression ($p < 0.05$) for which coefficients of determination (r^2) are given for each relationship.

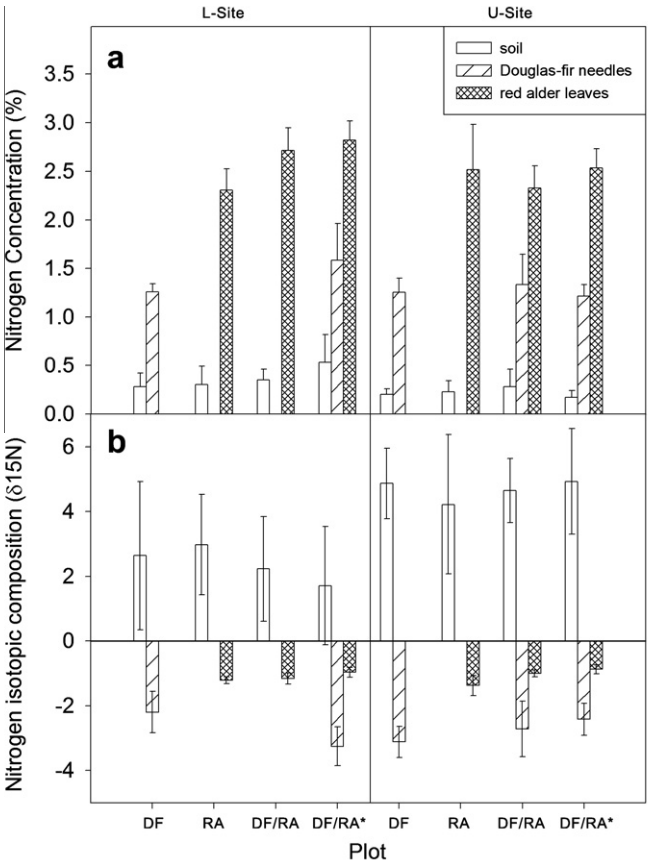

Fig. 7. The (a) nitrogen concentration (%) and (b) isotopic composition (δ15 N, ppt) in the soil (open bars), Douglas-fir needles (diagonal hatched), and red alder leaves (cross hatched) in each plot in at the L-site (left) and U-site (right). Douglas-fir = DF, red alder = RA, Mixed = DF/RA, mixed-delayed = DF/RA*. Error bars are one standard deviation from the mean.

4. Discussion

Despite the generally mesic climate in the western Cascade Mountains of Oregon, minor differences in site microclimate and fertility led to sizable differences in tree productivity. In mountainous regions, topographic heterogeneity in NPP is well-documented (Running, 1984). By contrast, the effect of site microclimate conditions on transpiration was relatively conserved, even in stands with different density or species composition. While leaf area index was a good predictor of tree productivity across sites (Luo et al., 2004), it did not explain much variability in transpiration; however, basal area was the best predictor of individual tree water use irrespective of site or species. Plots growing in wet cool settings generally will have greater LA:SA than those in drier warmer settings (Mencuccini and Grace, 1995). Our LA:SA estimates at the U-site were similar to those previously reported (McDowell et al., 2002), but were only weakly related to transpiration. It is likely that forests growing in wet environments are not optimized for water conservation. By contrast, in semi-arid climates, water availability is the primary driver of site productivity because of trade-offs between optimal growth and minimized water stress (Caylor et al., 2009).

Resource availability likely plays a major role in determining the strength of species interactions (Maestre et al., 2009). Nutrient and soil moisture limitations may have enhanced net competition in mixed plots at the U-site, where productivity was lower overall. The L-site, by contrast, had almost twice the soil N concentration and has a north-facing aspect with moister soils. In a larger set of experimental plots comparing this same location to another site located in a wetter climate, Radosevich et al. (2006) concluded that poorer site conditions were the likely reason why mixtures of Douglas-fir and red alder were more productive than monocultures under certain planted proportions. However, our subset of plots showed no consistent trends in transpiration or productivity with species composition.

Although water may not have been limiting much of the year, WUE was driven by local factors. WUE is an important measure of the resources plants need to grow and provides insights into how productivity and water use are linked. Landscape-level water use by plants can impact stream flow (Bond et al., 2002). Our results would suggest that you can reduce water use by shifting species composition (provided biomass is decreased), but it probably would not affect WUE. This has important implications for water resource management (Vanclay, 2009). The relationship between productivity and transpiration did not differ between species in monoculture plots or in mixtures. It is possible that the net effects of species mixtures on resource use are conserved and instead are an indirect consequence of altered plot biomass—future studies are needed to better shed light on this notion.

Although we did find some evidence of temporal partitioning of water utilization between Douglas-fir and red alder, it did not result in greater transpiration in mixed stands compared with monoculture stands. Peak sap flow in red alder occurred in late May while Douglas-fir continued to reach peak rates through early July, possibly indicative of greater sensitivity to soil moisture by red alder later in the season (Minore, 1979; Shainsky et al., 1994); conversely, initial spring increases in sap flow were later in red alder than Douglas-fir, probably because alder had not yet attained full leaf elongation. Douglas-fir transpiration was very low in the winter season, despite evergreen leaves, because of persistent cool and wet weather conditions that maintained low vapor-pressure deficit. Furthermore, even though evidence from this study suggests that red alder was fixing nitrogen, we found no evidence that Douglas-fir benefited from red alder. Red alder plots had soil nitrogen concentrations similar to those of all other plots, which may explain why all plots at a given site followed similar trends.

In conclusion, this experiment provided the opportunity to test for the effects of relative growth and mortality, species mixtures, and site conditions on water use. We found that the greatest variability in both productivity and transpiration was determined by site conditions and to a lesser degree, species composition. Despite marked seasonal and physiological differences, Douglas-fir and red alder performed similarly, because winter transpiration rates of evergreen trees were low. Leaf area index, which was much higher at the site with higher fertility, determined 70% of the variation in TBI. On the other hand, site conditions were the only determining factor for WUE. These trends suggest that forest managers could evaluate site characteristics independently for both productivity and resource use. An estimated 55% of precipitation on United States forest land is lost to evapotranspiration (Wiegand et al., 2009); thus, these results provide valuable scientific input for land-managers seeking effective strategies to maximize productivity while minimizing impacts on water resources.

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